ABIOTIC FACTORS AFFECTING SUMMER DISTRIBUTION AND MOVEMENT OF MALE PADDLEFISH, *POLYODON SPATHULA*, IN A PRAIRIE RESERVOIR

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ABSTRACT—Six male paddlefish, *Polyodon spathula,* were implanted with ultrasonic temperature-sensing transmitters and tracked during June through August 1997 to quantify effects of physicochemical conditions on their distribution and movement in Keystone Reservoir, Oklahoma. Paddlefish moved about twice as much during night than day. Movement rate of paddlefish was related to reservoir water level, inflow, and discharge from the reservoir at night; however, none of these variables was significant during the day. Location in the reservoir (distance from the dam) was negatively related to water level and positively related to inflow during day and night periods. Location in the reservoir was negatively related to discharge during the day. Paddlefish avoided the highest available water temperatures, but did not always avoid low dissolved oxygen concentrations. Paddlefish avoided the Cimarron River arm of the reservoir in summer, possibly because of high salinity. Our study demonstrates that distribution of paddlefish during summer and movement in Keystone Reservoir was influenced by physicochemical and hydrologic conditions in the system. However, biotic factors (e.g., food availability) not measured in this study may have been influenced by abiotic conditions in the reservoir.

RESUMEN—Se implantaron transmisores ultrasónicos sensores de temperatura a seis machos de *Polydon spathula* y se les siguió de junio a agosto de 1997 para cuantificar los efectos de las condiciones fisicoquímicas en su distribución y movilidad en Keystone Reservoir, Oklahoma. *Polydon spathula* se trasladó dos veces más durante la noche que durante el día. La tasa de movimiento de *P. spathula* estuvo relacionada con el nivel del agua de la reserva, entrada de agua, y descarga de la reserva durante la noche; sin embargo, ninguna de estas variables fue significativa durante el día. La localización en la reserva del *P. spathula* (distancia de la presa) estuvo relacionada negativamente al nivel del agua y positivamente relacionada a la entrada de agua durante los periodos del día y la noche. Su localización en la reserva estuvo negativamente relacionada a la descarga durante la noche. *Polydon spathula* evadió las más altas temperaturas del agua disponibles, pero no siempre evadió bajas concentraciones de oxígeno disuelto. *Polydon spathula* evadió la rama de la reserva del Cimarron River en el verano, posiblemente por la alta salinidad. Nuestro estudio demuestra que la distribución durante el verano de *P. spathula* y su movimiento en Keystone Reservoir estuvo influenciado por condiciones fisicoquímicas e hidrológicas en el sistema. Sin embargo, factores bióticos (e.g., disponibilidad de comida) no medidos en este estudio pudieron también haber sido influidos por las condiciones abióticas en la reserva.

The paddlefish, *Polyodon spathula,* is native to large free-flowing rivers of the central United States where they thrive in backwaters, oxbows, and deepwater channel habitats. In spring, paddlefish in large rivers make extensive spawning migrations (Russell, 1986), moving among pools during high water and associating with tailwater (when dams are present) and turbulent main-channel border habitats (Southall and Hubert, 1984; Moen et al., 1992). Over the past several decades substantial populations of paddlefish have developed in reservoirs of large rivers (Russell, 1986). Paddlefish presumably exhibit springtime movement and habitat use patterns in reservoir systems comparable to those in large river systems (Combs, 1982; Paukert, 1998); however, we know little about summer distribution and movement patterns of paddlefish in reservoirs.

Habitat preferences of paddlefish during the spring spawning period are generally understood (Hubert et al., 1984; Southall and Hubert, 1984; Crance, 1987; Brandtly, 1987; Moen et al., 1992); however, summer habitat requirements are less well known, particularly in reservoirs. Because of the diverse and unpredictable physicochemical habitats that paddlefish occupy, due in part to anthropogenic alterations (impoundment, regulated flows) of riverine environments, there is a need to determine habitat preferences of paddlefish under a variety of environmental conditions (Moen et al., 1992) and during seasons other than spring. To our knowledge, no one has examined the physicochemical and hydrologic factors influencing summer distribution and movement of paddlefish in reservoir environments.

Keystone Reservoir is a prairie impoundment in northcentral Oklahoma with an established paddlefish population and diverse physicochemical and hydrologic conditions. For example, the Cimarron River arm of Keystone Reservoir has salinities about four times higher than those in the Arkansas River arm, which creates a salt-heavy underlayment of water in the reservoir during summer (Eley, 1967). Little is known about salinity preferences of paddlefish. W. H. Neill et al. (in litt.) determined that paddlefish avoid high salinity levels in the laboratory; however, no concurrent field studies were conducted. In contrast, paddlefish tagged in Texas appeared to move through salt water and have been recaptured in Louisiana (B. Reed, Louisiana Department of Wildlife and Fisheries, pers. comm.). Our objective was to determine physicochemical and hydrologic factors affecting summer distribution and movement of paddlefish in Keystone Reservoir.

METHODS—*Study Site*—Keystone Reservoir is a 10,600-ha impoundment of the Arkansas and Cimarron rivers in northcentral Oklahoma with a maximum depth of 23.3 m and a mean depth of 7.7 m. In spring and summer, large water-level fluctuations (>4 m) are common due to unpredictable inflows into the reservoir and outflows for flood control and power generation. Surface water temperatures can be extreme, reaching 34°C. Keystone Reservoir becomes thermally and chemically stratified in summer, with higher salinity concentrations in the hypolimnion. The Cimarron River drains highly mineralized subsurface deposits of natural salts and gypsum in western Oklahoma producing high conductivity levels in the Cimarron River arm (Eley, 1970). The Arkansas River drains the southern plains of Colorado and Kansas and has high concentration of calcium and magnesium sulfate (Eley, 1970). The Salt Fork of the Arkansas River, a major tributary, is heavily influenced by naturally occurring salt flats in northwestern Oklahoma.

Field Collections—We captured paddlefish in monofilament gill nets (Paukert and Fisher, 1999) fished overnight on 1 and 6 March 1997. Fish were implanted with crystal-controlled, temperature-sensing ultrasonic transmitters (Sonotronics, Tucson, Arizona) with a 24-month battery life and a range of 3,000 m. Ultrasonic transmitters were chosen over radio transmitters (Fisher and Wilkerson, 1997) because of the high conductivity levels (up to 5,000 μS/cm) in the reservoir. Each transmitter had a unique aural code set at a frequency of either 74.0 kHz or 76.0 kHz allowing identification of individual fish. Captured fish were placed in a 538-l holding pen and weighed, measured (eye-to-fork length [EFL]; Ruelle and Hudson, 1977), and jaw-tagged with an individually numbered monel tag. Transmitter implantation procedures were similar to those described by Hart and Summerfelt (1975) with minor modifications (Paukert, 1998). We implanted transmitters in six male paddlefish (range, 843-1,000 mm EFL, 11.5–19.0 kg) on 2 and 7 March 1997. No females were collected, presumably because these fish and the larger males had moved up the rivers to spawn just prior to our sampling efforts (Paukert, 1998). Surgery time ranged from 8 to 12 min. Fish were then held in the water at boat side until they were able to swim off under their own power. Fish were monitored for about 30 min afterwards to verify movement away from the boat.

We searched the lower Keystone Reservoir system for transmitter-tagged fish by boat during June to August 1997 with a digital receiver (Sonotronics model USR 5W) and directional hydrophone (Sonotronics model DH-2). Periodic monitoring of fish from March to May 1997 was conducted to determine spring spawning migrations (Paukert, 1998). Paddlefish were tracked for this study at 3-h intervals from 0700 to 1900 h on 17 to 19 June, 30 June to 2 July, and 28 to 30 July, and were tracked from 2100 to 0600 h on 6 to 8 July, 3 to 5 August, and 10 to 12 August. Fish were located no more than once during each 3-h period. Keystone Reservoir was systematically searched for transmitter-tagged paddlefish beginning at the area where the fish were last located (usually the Arkansas River arm); most of the fish remained in the same general area (within about 5 km of each other). When all fish were not located within the 3-h period, we attempted to search the

TABLE 1—Categories of water temperature and dissolved oxygen for each of the three sampling periods used in water chemistry analysis of Keystone Reservoir. Nighttime sampling periods of 6–8 July, 3–5 August, and 10–12 August 1997 were removed from analysis because of uniformity of temperatures or low sample size.

Date	Temperature (°C)				Dissolved oxygen (mg/l)			
	Low	Moderate	High	Range	Low	Moderate	High	Range
17–19 June 1997	<24	24–25	>25	22–26	<4	4–6	>6	0–8
30 June–2 July 1997	<27	27	>27	26–28	<5	5	>5	2–6
28–30 July 1997	<27	27–29	>29	26–32	<5	5–7	>7	0–12

entire reservoir. A global positioning system receiver (Geoexplorer II, Trimble Navigation Inc., Sunnyvale, California) was used to determine geographic coordinates of the transmitter-tagged fish when we could hear the signal equally in all directions.

At each fish location, water temperature, dissolved oxygen (DO), and conductivity were measured at 1-m depth intervals with a multi-parameter water quality meter (model H20, Hydrolab Inc., Austin, Texas). When more than one fish was located in close proximity to another (<500 m), only one profile was taken. To characterize water chemistry conditions throughout the reservoir, we classified Keystone Reservoir into six areas, based on a previous temperature study of the reservoir (A.V. Zale et al., in litt.), and recorded water chemistry profiles in each of the six areas during each 3-day period when paddlefish were monitored. Hydrologic data (reservoir water level, discharge from the dam, inflow into the reservoir) were collected from the United States Army Corps of Engineers Keystone Dam facility.

Point locations of fish were overlaid onto a map of the reservoir using geographic information systems software (ARC/INFO, Environmental Systems Research Institute, Inc. Redlands, California). Movement rates were then calculated by measuring the shortest over-water distance between two points. To determine fish position within the reservoir, 500-m sections of the reservoir were measured at intervals along the centerline of the reservoir starting at the dam. Locations were then overlaid onto the 500-m grid to determine how far the fish was from the dam.

Because water chemistry differed among reservoir areas during the study, areas could not be combined to obtain overall available water chemistry conditions in the reservoir. Water chemistry conditions changed between each 3-day sampling period, but remained relatively constant within each period. Thus, we combined areas in which fish were located by arbitrarily categorizing water temperature and DO data as high, moderate, or low (Table 1). Areas of the reservoir were combined to include at least one vertical meter of the same temperature or DO category. For example, when we categorized moderate temperatures as 24–25°C, all areas that fish were located in during a 3-day period had at least one vertical meter with a temperature from 24–25°C. To select or avoid a certain water chemistry category, a fish would need to move vertically within an area. To remain in the same category, a fish could move laterally among areas.

To address the problem of pseudo-replication in movements, White and Garrott (1990) suggested that observations are independent if an animal has enough time to move from one end of its home range to another. The summer home range for a paddlefish was determined to be the entire area of Keystone Reservoir it occurred in throughout the study period. The overall linear distance of the home range (20.8 km) was calculated and divided by the maximum movement rate of the fish (4.1 km/h). Thus, the minimum time it would take for a fish to cover the entire home range was determined to be 5.1 h. Using this criterion, all repeated observations ≤5.1 h for the distance from the dam and water chemistry measurements were excluded.

Statistical Analyses—A Wilcoxon rank sum test was used to compare movement rates (m/h) for daytime and nighttime periods and for upstream and downstream movement rates. Spearman rank correlations were used to determine relationships between movement rates and distance from the dam to inflow, discharge, and water level. Correlations were used in lieu of regressions because we measured only abiotic variables and did not want to infer causation based on these factors alone. Movement was categorized as either upstream, downstream, or static (movement of less than a 45 degree angle from the main channel axis). Water temperatures where the fish was located were recorded from the implanted temperature-sensing transmitters. Depth, conductivity, and DO levels where the fish was located were determined by comparing the temperature from the transmitter with the corresponding water chemistry profile values from that area. Chi-square analysis was used to determine if fish selected or avoided areas of the reservoir based on temperature or DO conditions. Bonferroni multiple comparison procedures were used to determine differences among water chemistry categories (Neu et al., 1974). All analyses

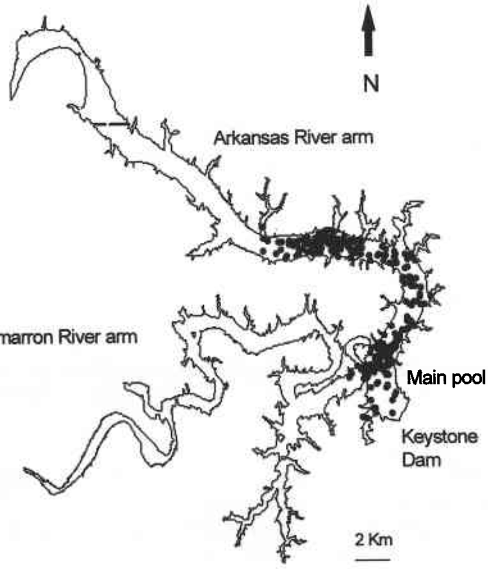

FIG. 1—Locations of transmitter-tagged paddlefish, *Polyodon spathula*, in Keystone Reservoir, Oklahoma, summer 1997.

were performed with SAS (Schlotzhauer and Littel, 1987); significance levels were set at $P \leq 0.05$.

RESULTS—Fish moved considerable distances (>500 m) soon after implantation. Because these movements were similar to movements encountered throughout the study, we assumed no short-term effects of surgery. All fish were located throughout the study period; however, not all fish were found during each 3-h interval. Fish congregated in the Arkansas River arm and the main pool of Keystone Reservoir. Although we searched the Cimarron River arm when we did not find all fish in other reservoir areas, we located no transmitter-tagged paddlefish upstream from the extreme lower Cimarron River arm (Fig. 1).

Water temperature, dissolved oxygen, and conductivity were recorded each sampling period in the Arkansas River arm and the main pool; however, these variables could not be recorded in the Cimarron River arm (the area not used by paddlefish) during all sampling periods because of time limitations. We were able to collect these data from the Cimarron arm for 17 to 19 June, 6 to 8 July, 28 to 30 July, and 10 to 12 August. From these data, we determined differences in water chemistry conditions between the two reservoir arms. Using water chemistry data, we quantified available habitat within the reservoir where paddlefish were located throughout the study (Arkansas River arm and main pool). All water chemistry data were included in analyses of movement rate and distance from the dam. When water temperatures were uniform in the reservoir, we were unable to infer depth, DO, and conductivity from the temperature-sensing transmitters. Uniform nighttime temperatures occurred on all sampling periods except 10 to 12 August; thus, we excluded nighttime periods from our water chemistry selection analysis because of small sample size ($n = 31$). All daytime periods exhibited thermal stratification and were used in all analyses.

Movement and Distribution—Paddlefish moved significantly more at night ($\bar{X} = 784$ m/h, $SD = 830$) than during the day ($\bar{X} = 348$ m/h, $SD = 248$; $P < 0.001$). Movement rates were highly variable, ranging from near 0 m/h during the day to 4,007 m/h at night. Daytime movement rates ($n = 120$) were not related to water level, inflow, or discharge (all rs between -0.03 and -0.13, all Ps > 0.165); however, nighttime movement rates ($n = 86$) were negatively related to discharge ($r = -0.44$, $P < 0.001$, inflow ($r = -0.41$, $P < 0.001$) and water level ($r = -0.57$, $P < 0.001$). Although nighttime paddlefish movement was associated with decreased discharge, inflow, and water levels, all three hydrologic variables were correlated to each other (all rs > 0.48, all Ps < 0.001) in the movement rate analysis. Paddlefish showed no difference in movement rates upstream or downstream ($P = 0.253$).

During the day ($n = 93$), distribution of paddlefish (distance from the dam) in the reservoir was negatively related to water level ($r = -0.59$, $P < 0.001$) and discharge ($r = -0.61$, $P < 0.001$), and positively related to inflow ($r = 0.53$, $P < 0.001$). Similar relationships were found with paddlefish location at night ($n = 70$) with water level ($r = -0.60$, $P < 0.001$) and inflow ($r = 0.28$, $P = 0.019$). However, the relationship between discharge and paddlefish distance from the dam at night was not significant ($r = 0.20$, $P = 0.091$). In this analysis, the three hydrologic variables were correlated for both day and night periods. Inflow was negatively related to water level ($r = -0.41$, $P < 0.001$, $n = 93$) and discharge ($r = -0.45$, $P < 0.001$, $n = 93$) during the day, and positively related to water level ($r = 0.33$, $P = 0.005$, $n = 72$) and discharge ($r = 0.92$, $P < 0.001$, $n = 72$) during the night. Water level was positively related to discharge during the day ($r = 0.91$, $P < 0.001$, $n = 93$) and night ($r = 0.36$, $P = 0.002$, $n = 72$).

Habitat Preferences—Water temperature varied throughout the study period; therefore, we analyzed water temperature preferences for each 3-day period independently. Conductivity data were not categorized because of low variability at sites where paddlefish were located. Consequently, chi-square analysis was not performed on this variable.

Paddlefish selected moderate temperatures in the reservoir throughout the study period. Paddlefish selected 24–25°C temperatures and avoided temperatures <24°C and >25°C on June 17–19 ($P < 0.001$). On 30 June to 2 July, paddlefish selected 27°C and avoided temperatures >27°C, but showed no selection for temperatures <27°C ($P < 0.001$). Fish avoided temperatures <27°C and >29°C on 28–30 July and selected for 27–29°C temperatures ($P < 0.001$).

Paddlefish selected water with DO concentrations of 4–6 mg/l, avoided DO >6 mg/l and showed no selection for DO <4 mg/l on 17–19 June ($P = 0.002$). On 30 June–2 July and 28–30 July, paddlefish avoided DO levels >5 mg/l and selected for DO <5 mg/l ($P < 0.001$) waters.

Paddlefish appeared to avoid the high salinity of the Cimarron River arm of Keystone Reservoir. Temperature and dissolved oxygen profiles were similar between the Arkansas and Cimarron River arms, but conductivity levels were much higher in the Cimarron River arm. Mean temperatures for the Arkansas River arm ranged from 25.2 to 29.3°C ($SD = 0.7$–1.8); corresponding means for the Cimarron River arm ranged from 26.6 to 28.4°C ($SD = 0.6$–1.3). Dissolved oxygen concentrations varied within the Arkansas River arm ($\bar{X} = 3.4$ to 5.8 mg/l, $SD = 1.0$–2.5) and Cimarron River arm ($\bar{X} = 1.4$ to 6.3 mg/l, SD 1.3–2.6). Conductivity levels in the Cimarron River arm averaged about 2–3 times higher than those of the Arkansas River arm (Fig. 2); mean conductivity readings were 772 μS/cm ($SD = 155$) in the Arkansas River arm, 995 μS/cm ($SD = 477$) in the main pool, and 1,914 μS/cm ($SD = 1{,}125$) in the Cimarron River arm. Main pool conductivity levels were intermediate and highly variable because of the influence of the Cimarron River as it joined the Arkansas River at their confluence. Paddlefish were not observed in mean conductivities greater than 1,275 μS/cm (Fig. 2). About 50% of the observations were in mean conductivities less than 700 μS/cm and 50% were in mean conductivities between 700 μS/cm and 1,275 μS/cm.

Discussion—Distribution and movement of male paddlefish in summer is influenced by physical and chemical characteristics of their environment. However, our results are based on only six male paddlefish. Although these fish did not make the spawning migration, they did have enlarged testes, suggesting they were sexually mature. Most female paddlefish appear to make an upriver spawning migration in Keystone Reservoir during spring; however, even some large, (>1,000 mm EFL), and presumably mature, male paddlefish remain in the reservoir during the spawning migration (Paukert, 1998). Female paddlefish may exhibit other physiological requirements that may influence their summer distribution and movement. Because we only implanted male paddlefish, inferences to distribution and movement of female paddlefish may be inappropriate.

Brandtly (1987) found that summer movement of paddlefish in a run-of-the-river reservoir in Alabama was affected by water temperature and very high discharge, but movement was not affected at moderate discharge levels. Movement of paddlefish in Keystone Reservoir was related to water level, inflow, and discharge at night, and not related to any hydrologic variables during the daytime. This pattern may be related to their feeding behavior. Paddlefish generally feed at night (Ruelle and Hudson, 1977), and zooplankton availability may be influenced by their vertical distribution in relation to hydrologic changes in the reservoir. Furthermore, movement rates of paddlefish increased at night, possibly suggesting they were actively feeding during this time.

Upstream orientation and movement in response to increased flows is common among many fish species (McKeown, 1984; O'Hara, 1993). However, riverine fish also may move downstream as water levels and discharge increase (Hynes, 1970), presumably to seek more

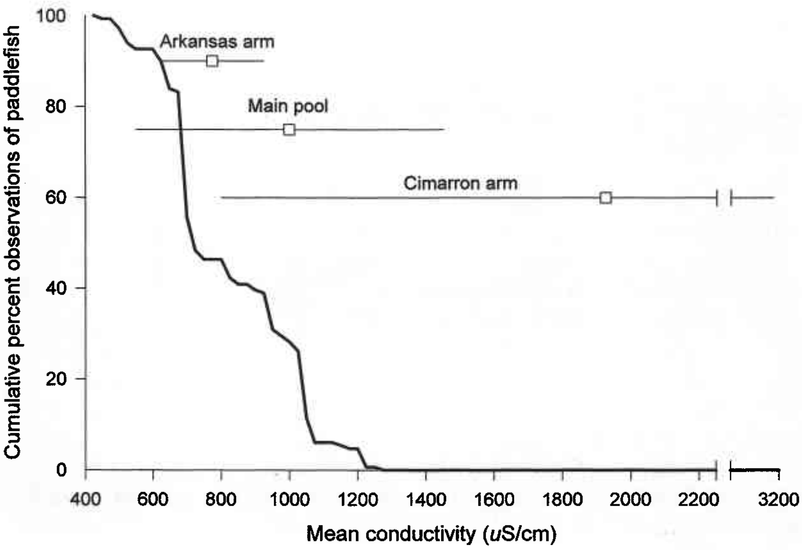

FIG. 2—Mean conductivity levels in Keystone Reservoir, Oklahoma, in relation to cumulative percent paddlefish, *Polyodon spathula*, observations. For example, 100% of paddlefish observations occurred at conductivity levels >400 μS/cm, and no paddlefish were observed at levels >1,275 μS/cm. Squares are mean conductivity levels and horizontal bars are 1 *SD*.

favorable environmental conditions or food resources (McKeown, 1984). Distribution of paddlefish in Keystone Reservoir was related to water level changes. As water levels increased, paddlefish moved closer to the dam, and as water level decreased, paddlefish moved up the Arkansas River arm of the reservoir. Southall and Hubert (1984) found no response to water level changes in summer by paddlefish in the Mississippi River. In this study, paddlefish were further away from the dam when discharge decreased during the day. The opposite (albeit relatively weak) relationship existed during the night. However, Moen et al. (1992) found no relationship between discharge and direction of movement of paddlefish in the Mississippi River. In contrast, paddlefish are strongly influenced by water flow and river stage during spring migrations (Russell, 1986; Paukert, 1998). Summer downstream movements of paddlefish in Keystone Reservoir may be attributable to an innate response by riverine fishes to avoid harsh environmental conditions (McKeown, 1984), such as poor water quality. Extreme water temperatures, low dissolved oxygen, and high salinities are typical of prairie rivers during low flow periods in summer.

Hydrologic variables also may influence longitudinal zonation of zooplankton. It is possible that relationships we found between paddlefish distribution and movement and hydrologic variables may be an indirect response of paddlefish following food resources. Zooplankton densities in reservoirs typically are highest in middle areas and low in upper reaches because high current velocities are too great to promote adequate zooplankton reproduction (Marzolf, 1990). Low zooplankton densities are also common in lower reaches where nutrients settle to deeper water or are consumed (Marzolf, 1990). Similarly, Kochsiek et al. (1971) found high zooplankton densities in the middle of each arm of Keystone Reservoir.

Paddlefish distribution in Keystone Reservoir was related to temperature and dissolved oxygen. During the day paddlefish avoided the highest water temperatures near the surface and usually selected for moderate temperatures. Rosen and Hales (1981) determined the optimum temperature for paddlefish feeding was from 7 to 20°C, but that fish occurred in temperatures up to 28°C. Blackwell et al. (1995) found that paddlefish fed at temperatures greater than 20°C. Crance (1987) showed that optimum temperatures for paddlefish were between about 12 and 24°C. Keystone Reservoir paddlefish, however, selected water temperatures that ranged from 24 to 29°C.

Although paddlefish appeared to avoid high DO levels, the strong correlation between surface water temperatures and dissolved oxygen suggests they were avoiding high water temperatures and not DO levels. Although no information exists on the minimum DO requirements for adult paddlefish, Fry (1971) determined that DO concentrations less than 5 mg/l affect swimming speed, growth, feeding, and blood chemistry in some teleost fishes. Adult paddlefish may not require high (>6 mg/l) DO concentrations and can survive at DO levels less than 5 mg/l.

Paddlefish appeared to avoid the Cimarron River arm of Keystone Reservoir during the entire study period. The morphometry of the lower Cimarron River arm, main pool, and lower Arkansas River arm are similar; however, conductivity levels were much greater in the Cimarron River arm. The lack of paddlefish locations in the Cimarron River arm may be attributable to their avoidance of higher salinity levels in this arm of the reservoir. W. H. Neill et al. (in litt.) found that juvenile paddlefish avoided salinities greater than 4 ppt when available.

Food availability was not examined in this study; however, we do not believe that food was a limiting resource in the Cimarron River arm. Kochsiek et al. (1971) found a greater density of zooplankton in the Cimarron River arm, but similar zooplankton diversity between both arms of Keystone Reservoir. He attributed a lack of certain rotifer species in the Cimarron River arm to high conductivity levels, which may have limited their distribution. Paddlefish are known to be indiscriminant feeders (Rosen and Hales, 1981). Therefore, we do not believe paddlefish selected the Arkansas River arm over the Cimarron River arm because of food preference or availability. The only time paddlefish were located in the Cimarron River arm (i.e., 1 km upstream from the confluence) was when high flows from the Arkansas River backed up water into the Cimarron River arm and reduced conductivity levels. The confluence of the Cimarron and Arkansas rivers produces a circular current in which the Arkansas River arm water flows up the Cimarron River arm and then returns to the Arkansas River arm (Kochsiek, 1970). Paddlefish do, however, occur in the Cimarron River arm during other seasons. Paddlefish stage in the Cimarron River arm in late winter and move up this tributary in spring, presumably to spawn (Paukert, 1998).

Paddlefish distribution and movements in Keystone Reservoir were influenced by hydrologic factors in summer. Furthermore, paddlefish distribution may be limited by physicochemical conditions (i.e., high salinity levels and water temperatures), precluding their use of certain areas of the reservoir. Although we only measured abiotic factors, biotic factors (e.g., food availability) most likely play a vital role in paddlefish distribution and movement. Further work is needed to evaluate effects of physical, chemical, and biological factors on paddlefish distribution and movements in reservoir environments, particularly during summer.

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